Observations upon the Behaviour and Structure of Hydra.

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With 4 Text-figures.

Contents.

Introduction.

The Hydras upon which the following observations were made were obtained from various sources, chiefly through the kindness of Dr. Monica Taylor, from the Convent of Notre-Dame. They were kept in covered, half-pint glass tumblers, in water from a large tank in which there was a fair quantity of weed and a variety of animal life (Isopods, Cladocerans, Planarians, &c.). This was used because the Hydra would not live for more than one or two days in tap-water. The water was changed and the tumblers cleaned when necessary. This was about once a week in summer, as food-remains became foul very quickly then, but less frequently in winter. The water was never aerated artificially. The Hydras were fed on a culture of Daphnia twice a week, and the remains and excreta removed, as far as possible, the following day. Under

these conditions the Hydras lived and remained healthy for months. Occasionally one or two, for no apparent reason, would decrease in size and finally degenerate and die, but in only one case was a whole tumbler attacked by a ' depression period '. Even here a fair proportion remained healthy throughout. When well fed the Hydras budded actively. None of my specimens carried more than four or five buds at a time and the number was usually less.

Sexual reproduction took place in autumn and in early summer. The animals were hermaphrodite. With the exception of four specimens, not differing outwardly from the rest, all those which produced eggs produced testes at the same time. Testis formation usually began before egg formation in any individual. Many specimens showed testes without eggs, but as egg production entails a considerably larger expenditure of energy and food material than testis production, this is not surprising. The four exceptional, apparently female, specimens were kept under observation for about eight weeks, but died before undergoing another sexual period. Three or four eggs were sometimes formed at one time, although they might not all attain full size and break through the ectoderm.

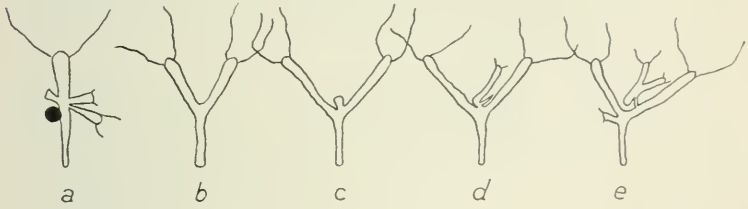
One large and healthy specimen showed four eggs developing and a number of testes. Three of the latter had developed in the ectoderm of three tentacles. One testis was just at the root of a tentacle, another a little further out, and the third at a distance from its base of about quarter the length of the tentacle. The testes were ripe and spermatozoa were swarming in them. In this animal interstitial cells must have been present in the tentacles, which is not usually the case.

The period from the freeing of the egg to the hatching of the young Hydra varies with the season. A batch of eggs set free in November hatched in January, while some produced in summer took only about three weeks to develop. In many cases the eggs failed to hatch owing to the attacks of bacteria or fungi. The young Hydra emerges by a crack in the shell, usually equatorial. It is oval and almost colourless, but in

a few minutes it stretches out and extends little projections which develop into tentacles during the next twenty-four hours. It is then able to feed. The rupture of the shell suggests the formation of a hatching ferment, such as has been described in Lepidosiren and Teleostean fishes (**15**).

Abnormalities are not uncommon among newly hatched Hydras, possibly due to injuries during hatching. Several two-headed specimens appeared, the double part varying in length. Such specimens are not infrequent among adult Hydras. In one or two cases the division appears to be growing gradually deeper, so that eventually the compound would split

Text-fig. 1.



into two separate Hydras, but in most cases the specimens remained without change for weeks and died without further division. In no case was there any suggestion that a process of fusion was going on. In two specimens the hypostome only was double and several of the tentacles belonged to both rings.

The origin of a double Hydra can sometimes be observed (Text-fig. 1). One normal specimen produced two buds close together (Text-fig. 1, *a*), and in the course of development these grew out on a common stalk. Although one of the buds was a day or two younger than the other, they soon grew to equal size. This double individual then separated (Text-fig. 1, *b*) from the normal parent, and a week later both of its limbs produced normal buds which separated off. Two days later a third bud was formed near the junction of the two limbs (Text-fig. 1, *c*). The next day a curious pointed projection grew up between the bud and one limb (Text-fig. 1, *d*). Eventually this grew into a second bud joined to the first (Text-

fig. 1, *e*), and the whole was separated as a double Hydra. Unfortunately this specimen died before reproducing itself further. It should be noted that the mode of origin of the second half of the compound is distinctly abnormal.

Leiber (**8**) reports a case in which one component of a double Hydra, just before the division had reached the foot and the two were about to separate, itself divided again at the hypostome. It died before further observations could be made. These cases indicate that a tendency towards doubleness may be inherent in some Hydra stocks. From the infrequency and origin of these abnormalities and the frequent death of the compounds, it does not seem probable that longitudinal fission is a normal method of reproduction.

I have seen transverse fission take place only in obviously unhealthy specimens.

Hydras are sometimes found in which two or more tentacles are in process of fusion from the base upwards. This seems to be a method of regulating the number of tentacles to the size of the Hydra, for it is found chiefly in animals which are decreasing in size, or in those which have an exceptionally large number of tentacles for their size. The commonest numbers of tentacles were five, six, or seven, but some specimens showed as many as ten.

The appearance of an animal undergoing 'depression' has been so often described that it is unnecessary to do so here. In the early stages the Hydra may take on an appearance very different from its usual, the differences being sometimes those described as characteristic for another species.

For several months the Hydras I had were overrun with Kerona and Trichodina, but they seemed none the worse for it. This is contrary to the observations of P. Schulze (**9**), who states that Kerona caused depression in his animals.

Feeding.

The Hydras were usually fed on a culture of Daphnia, but were occasionally given Cyclops, Cypris, or small

insect larvae, all of which they ate readily. Simocephalus was also tried as a food, but the Hydra seemed unable to kill it. The Simocephalus were frequently caught and held struggling for an hour or more, but in the end they freed themselves and escaped uninjured. If killed and presented to the Hydra, they were eaten as readily as Daphnia. On three occasions a Simocephalus was captured and eaten by a Hydra. In the first case the animal remained alive inside the Hydra for a considerable time and could be seen moving its antennae. A second was caught and digested immediately after ecdysis. I have, however, seen a Hydra catch a Simocephalus which then underwent ecdysis and was immediately recaptured, yet eventually freed itself. When caught, the contrast between the behaviour of Daphnia and of Simocephalus is remarkable. The Daphnia struggles violently for a few minutes, then the heart stops beating and the animal soon succumbs although the antennae may keep up a quivering movement for some time longer. If freed from the Hydra, it does not recover. Simocephalus, on the other hand, continues to live and to struggle at intervals until it frees itself. The heart continues to beat the whole time. The cuticle of Simocephalus is not appreciably thicker than that of Daphnia. It may be more resistant to the entry of the nematocysts, or the tissues of the animal to the action of their poison. When both Daphnia and Simocephalus are immersed in dilute solutions of poisons (such as formic acid, or chloroform) Simocephalus succumbs first.

Schulze (**9**) mentions that in a culture of H. circumcincta a Daphnia sometimes stuck on to the tentacles and was dropped again uninjured. It is perhaps possible that these were really Simocephalus also, for the two genera are closely similar and may be mistaken for one another unless carefully examined.

The capture of the food generally seems to be a more or less passive action, any small object presented to the Hydra being seized and carried to the mouth. Indifferent substances

are usually dropped after a few seconds, although a few Hydras were induced to swallow pieces of white of egg (which were returned undigested in the course of twelve hours) and pieces of blotting-paper when soaked in blood.

If Daphnia is left in a weak solution of litmus for eighteen to twenty-four hours, the alimentary canal in the head-region usually takes on a pink tinge. If these stained animals are fed to Hydra, a colour-change from pink to blue takes place in those animals which show nematocysts sticking into the head-region. This may indicate an alkaline reaction for the nematocyst poison. The change takes place slowly, often after the death of the Daphnia, but does not occur when the animal is killed with a needle. Simocephalus does not take up the colour well, and often dies if left in the litmus solution for twenty-four hours.

The digestive juices of Hydra are alkaline, but have no effect on Hydra itself. I have seen one Hydra completely ingested by another, in whose cavity it remained for more than twelve hours. It was returned again none the worse. A tentacle is frequently swallowed along with the food to which it is sticking, and remains in the coelenteron for some hours, but comes out quite unaltered. One Hydra even went as far as to engulf about half its own body, beginning at the foot, where a Daphnia had stuck.

In many cases, particularly where the animal was attempting to swallow something exceptionally large, the hypostome was turned inside out over the tentacle-bases and remained so for some time. It rarely went further than this, but in one small regenerating specimen the process went on till the whole animal had turned inside out. It righted itself in the course of an hour. The converse also takes place sometimes, and the hypostome is turned inwards till it hangs down into the coelenteron. Both of these performances are of interest, inasmuch as a condition is assumed which has become permanent and normal in other types of Coelenterata, e.g. the trumpet-shaped hypostome of Obelia and the invaginated hypostome of the Actinozoa.

Reaction to Stimuli.

Hydras were tested to find out their reaction to mechanical and chemical stimuli.

Mechanical Stimulation was carried out with a glass rod drawn to a fine point.

Slight stimulation of a tentacle leads to contraction of that tentacle only. The tentacle often adheres to the rod for a few seconds.

Strong stimulation of a tentacle leads to its contraction over the mouth, when the other tentacles bend up till they meet and the head turns to one side, exactly as when catching prey (capture response). This response is sometimes obtained by rubbing on the insides of the tentacle bases, and sometimes by touching the oral cone. Strong stimulation of the oral cone leads to contraction.

Stimulation of the outsides of the tentacle bases and of the body in that region sometimes leads to contraction, but often has no result.

Gentle stimulation of the body generally has no result, but sometimes leads to contraction, as strong stimulation always does.

Stimulation of the foot always leads to contraction of the body (not of the tentacles, unless strong). This is probably an adaptive reaction to movements of the object to which the Hydra is attached. When contracted, the resistance to water will diminish, and the animal will be less liable to be torn off.

Gentle touches repeated at intervals of five seconds or two and a half seconds sometimes have no effect even when carried on for several minutes. More often they lead, first, to a swinging away of the body, and finally to contraction after a few minutes. In swinging away the body is bent just above the foot region. As the body remains quite straight the action must be confined to a small number of muscle-fibres in the region of the bend, which is usually in a different part of the body from the stimulation. This shows the existence of a conducting mechanism.

Chemical Stimulation.—When food, such as a piece

of Daphnia, is made to touch a tentacle tip, the capture response immediately takes place. The food is thus brought in to the hypostome ; and the tentacles, bending over, would prevent escape were it alive.

Chemical stimulation was also carried out with weak acetic acid coloured with methylene blue. The strength used was 0·025 per cent., but this was probably much weaker by the time it actually reached the Hydra. It did not injure the tissues appreciably.

Stimulation applied to Tentacle.—In about 60 per cent. of the cases the tentacle contracted and the capture response followed in about twenty seconds. In 30 per cent. of the cases the whole Hydra swung away after forty seconds, and in the remainder the animal contracted after about thirty seconds. In one case a repetition of the stimulus immediately after the response led to a second response without any pause.

Body.—The body, when stimulated, either contracted or swung away after thirty to forty seconds. In several cases there was no result.

Oral Cone.—When the oral cone was stimulated the body contracted, sometimes immediately, sometimes after thirty to forty seconds.

Foot.—Stimulation of the foot resulted in a general contraction of the body, but it was very insensitive, and out of eighteen stimulations twelve had no effect. In other cases the body contracted after an interval varying from fifteen to thirty seconds.

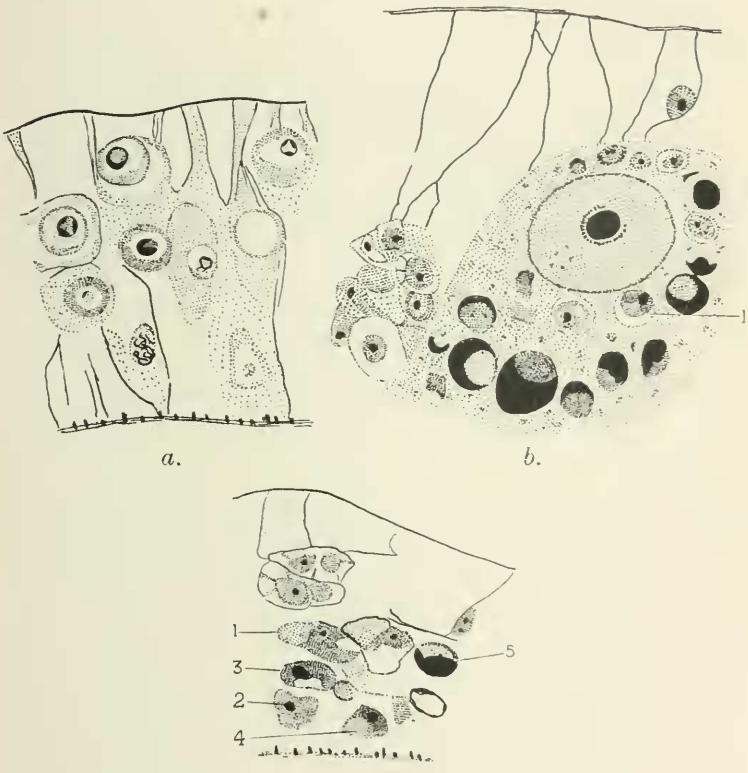
From the above it will be seen that the head and foot regions are much the most sensitive parts of the Hydra to mechanical stimuli, while the foot appears to be comparatively insensible to chemical stimuli, at least to acetic acid.

Egg Formation.

When the Hydra is about to form an egg the interstitial cells are multiplied enormously and form a mass bulging out the ectoderm. Characteristic changes take place in their

nuclei. The chromatin collects round the periphery of the nucleus, leaving the nucleolus in the centre of a clear space (Text-fig. 2, *a*). The nucleolus sometimes becomes difficult to stain, or only part of its periphery stains. Wager (13)

TEXT-FIG. 2.



Sections of ectoderm showing development of ovum.

believes that vacuoles form in it at this stage. Secondary nucleoli may make their appearance, often in large numbers. These may be droplets of food material as Wager suggests, for the cytoplasm is also full of darkly staining particles. At a stage just before the definite egg-cell becomes recognizable

several interstitial cells, much larger than the rest, may be seen undergoing nuclear changes. The chromatin has formed a thick spireme thread, and in some cases the nuclear membrane has disappeared. The nucleolus takes no part in this, but lies unchanged in the midst of, or to one side of, the spireme. This is in accordance with the observations of Wager, who states that 'the egg begins its growth by the coalescence of a group of the primitive ova; this process is frequently attended by a peculiar nuclear degeneration'.

Later the egg appears as a hemispherical mass of protoplasm with lobed edges, which lies with its base in contact with the mesogloea. The protoplasm is reticular, and at this stage contains none of the so-called 'pseudo-cells'. The nucleus corresponds in size with the cell and contains a large nucleolus and a number of smaller secondary nucleoli varying in size. The egg grows by the absorption of other interstitial cells, but at this stage the nuclei of the latter break down completely before absorption. The protoplasm of the egg is filled with minute deeply staining dots, probably, at least in part, the remains of the chromatin of the absorbed cells.

At a later stage (Text-fig. 2, *b*) the egg protoplasm is filled with a mass of degenerated cells ('pseudo-cells') and interstitial cell nuclei. Intermediate steps can be traced showing the process of degeneration of an interstitial cell. The process goes on both inside and outside the egg. In groups of interstitial cells, usually at some distance from the egg itself, the nucleus is seen in the centre of the cell, surrounded by a dense mass of protoplasm. The nuclear membrane is hardly visible or has disappeared entirely (Text-fig. 2, *c*, 1 and 2). This mass moves to one side and applies itself to the cell-wall as a densely staining mass (Text-fig. 2, *c*, 3 and 4). The nucleus is at first visible as a darker body, but eventually the whole mass stains so deeply that the constituent parts are indistinguishable (Text-fig. 2, *c*, 5). Groups of these degenerate cells are found in the ectoderm after the egg has separated and are possibly used up by a subsequent egg.

When the degenerative process takes place within the cyto-

plasm of the egg, it may go on much as described above (Text-fig. 2, *b*, 1), or the cytoplasm may, to all appearance, be absorbed directly into that of the egg and the nucleus alone undergo visible change. Wager (**13**) describes such degenerative products formed from whole cells, from nuclei, and from nucleoli. I have not seen any of the last named in process of formation, but from the small size of some of the masses it seems probable that this is the case in my specimens also. In several cases a nucleolus seemed to be breaking through the nuclear membrane of an interstitial cell.

These degenerative cells are looked on as stores of energy to be used up by the embryo during development. Tannreuther (**11**) states that they divide by amitosis after their absorption into the egg-cell, but I have seen no signs of this. It has been stated that they are all used up before the young Hydra hatches, but this is not the case, for large numbers are present in the tissues of newly hatched Hydras and they do not entirely vanish till some time after hatching.

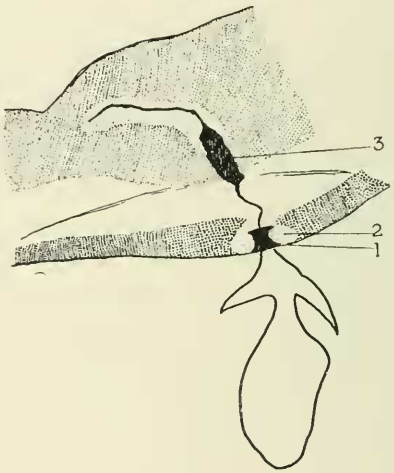
In my specimens the egg-shell is formed by a kind of vacuole formation at the surface of the egg. The edges of the vacuoles come in contact with one another, and their limiting membranes then harden to form the spicules. This is in accordance with the observations of Brauer (**2**) and Kleinenberg (**7**). The eggs then drop off and fall to the bottom.

Nematocysts.

The nematocysts have been much studied, and of late have been used largely to distinguish the different species of Hydra. There are four main types of nematocyst, large pear-shaped, small pear-shaped, and two types of cylindrical nematocysts which differ from each other in size and in the way the thread is coiled inside. As the two last are not always strictly cylindrical, and as the names in other respects are not suitable, Schulze (**9**) has proposed to name the different types from their functions as Penetrant, Volvent, and Glutinant. Otto van Toppe (**12**) was the first to study the functions of all three types in detail.

The large pear-shaped nematocyst is, as the name penetrant implies, used for piercing the chitinous exoskeleton of the prey. When the hard shell has been pierced, the thread is everted into the soft tissues beneath. Usually only that part of the nematocyst immediately above the large barbs succeeds in penetrating, but as the thread itself has a spiral coil of small hairs or barbs upon it, it is firmly held in place. The large barbs, which are so conspicuous a feature of the exploded

Text-fig. 3.



Discharged nematocyst.

nematocyst, are never found imbedded in the tissues of the prey. Iwanzoff (**6**) says that the three, just at the moment of their eversion, form a stiletto which pierces the cuticle of the prey, making a hole by which the thread can enter. With the further eversion of the thread the barbs swing outward to their final position. Some chemical action is exerted on the chitin, as can be seen from a study of sections. Immediately around the point of entry is a deeply staining area, irregular in form (Text-fig. 3, 1). This probably corresponds to an outpouring of the poisonous fluid contained in the nematocyst, for the thread stains in the same way. Outside this dark patch is

a bowl-shaped space which stains less deeply than the normal chitin (Text-fig. 3, 2). The thread can be seen lying in the soft tissues, the first part at right angles to the external surface. The distal part usually curves to one side. It is filled with a darkly staining mass which is extruded either at the end or along its course (Text-fig. 3, 3). In preparations of unfixed, exploded nematocysts stained in methylene blue, the fluid inside the penetrants stains deeply and can be seen partly inside the capsule and partly in the form of tiny drops on the outside of the thread. The thread has, apparently, rows of minute pores or permeable areas through which the fluid can escape, as well as by the opening at the end.

The threads of the small pear-shaped nematocysts, or volvents, when exploded, wind tightly round any protruding hairs or bristles on the prey, and so hold it captive till it has been killed by the poison of the penetrants. The thread is coiled inside the capsule in two loops which lie on one another so that they appear in section like one thick ring. There is a row of small hairs on the thread arranged in a very open spiral. When exploded, the thread coils up tightly, and in optical section there is seen to be a narrow space along the axis of the coils which is closely beset with hairs. This forms an efficient mechanism for grasping the bristle, and there is some evidence that the secretion in the capsule and thread, which stains deeply with methylene blue, is sticky. Van Toppe (**12**) states that the stimulus for the explosion of this type of nematocyst is different from that exploding the penetrants, as the latter explode when their cnidocils come in contact with flat surfaces, while the former do not.

The third and fourth types of nematocyst, the glutinants, are usually cylindrical. One type is usually larger than the other. In the former the thread shows four or five turns almost at right angles to the long axis of the capsule and below this is wound irregularly. In the latter the thread is wound in an irregular figure of eight. Schulze (**9**) therefore calls them streptoline and stereoline respectively. In some Hydras (e.g. H. attenuata, van Toppe, H. circumcincta,

Schulze, H. stellata, Schulze, and Pelmatohydra braueri, Schulze) the streptoline is not cylindrical but pear-shaped. When Hydra sticks on to glass or to any other surface by means of its tentacles or hypostome, it uses these nematocysts. If one of the adherent tentacles is examined, there are seen numerous exploded glutinants whose threads are firmly attached to the glass. They are so firmly fixed that if any pull is exerted on them the cell protoplasm of the Hydra is drawn out into a thread with the nematocyst at its tip. Zygoff (**16**) was the first to notice these, and looked on them as pseudopodia by which the animal moved. Toppe discovered their true nature. These processes can withstand a considerable strain. I have seen a Hydra apparently trying to free a tentacle which was held at the tip by one of these nematocysts only. The tentacle was given several tugs, was twirled round rapidly, first in one direction and then in the other, the animal contracted tightly once or twice, and finally the tentacle was torn away. It was striking to watch an animal like the Hydra exhibiting such apparently purposeful movements. The twirling movements are much more complex than any the Hydra usually shows, and must have called into play a different mechanism. The nematocyst is always left sticking to the substratum while the protoplasmic process is gradually withdrawn into the cell. A similar process is sometimes drawn out when a tentacle is pulled away from some bristle on which a volvent has wound itself.

In unfixed, exploded glutinants stained with methylene blue, numerous droplets can be seen on the outside of the thread, as in the case of the penetrants. This secretion is probably sticky, and possibly hardens in contact with water. When used, it is extruded not only by the pore at the end of the thread but also by the side pores, for the thread can often be seen adhering at a point about half-way down its course.

It seems probable that the secretion of the other types of nematocyst has also to some degree the property of sticking firmly. I have observed tentacles adhering both by the penetrants and by the volvents, though not so firmly.

The size of the nematocysts has been cited as a characteristic difference for the various species. Most authors, however, give relative sizes only, and all measurements are given for the penetrants alone, which, as will be seen, are much the most variable in size of all the types. Steche (**10**) states that the penetrants of H. fusca are at most 8–8·5 μ, and those of H. grisea at least 10·5 μ and usually 13–13·5 μ. Toppe (**12**) says that those of H. fusca are the smallest, H. grisea next, and those of H. attenuata the largest. Schulze (**9**) gives 25 μ for his H. attenuata (which is not the same species as Toppe's) and 13 μ for Pelmatohydra oligactis.

In my Hydra the size of the penetrant varies greatly. Some forms measure 10 μ or 11 μ and others may be as large as 22 μ. Even in one individual the sizes may vary by as much as 8 μ. The small penetrants are found in the tentacles as well as in the body and are not merely incompletely developed. It is difficult to speak with certainty, but the most frequent size seems to be about 15 μ; 12–13 μ and 18–19 μ are commoner than the intermediate sizes. In small Hydras the smaller size seems to be more frequent than the large.

The glutinants vary much less, the ranges of individual variation not being more than 3 or 4 μ. The larger type (streptoline) measures about 11·5 μ (maximum 13 and minimum 10 μ), and the smaller (stereoline) about 9 μ (7–11 μ).

The volvents measure from 5–10 μ. The usual size is about 8 μ and the smaller sizes are more numerous than the larger.

In order to see whether the size of the nematocysts varied from time to time with changes in the size of the individual, I took a large well-grown Hydra, and after removing two of the tentacles in order to measure the nematocysts, starved it for seventy-three days. The measurement of the width of the foot when the animal was fully extended was, before starvation, about 0·275 mm., and, after, about 0·100 mm. It had therefore decreased to almost a third of its original width, and this gives a rough indication of the general effect. Whereas, before starvation, the nematocysts were of normal size (penetrants

19 μ), the penetrants now measured only 11–15 μ. This was due, in the first place, to the disappearance of the large type. The other nematocysts, however, also showed a similar though slighter decrease in size. The same experiment with another Hydra (starved forty-seven days) yielded similar results. If the size of the nematocysts varies with the size or condition of the individual it is obvious that this cannot be used as a trustworthy characteristic in differentiating between the various species.

In Hydra viridis the penetrants measure 8–10 μ; the streptoline glutinants are kidney-shaped and are as large as the penetrants, being 10–11 μ. The stereoline glutinants are much smaller and rarer, being only 6–7 μ, and the volvents are about 5 μ.

To obtain the nematocysts freely the Hydra was at first macerated in weak chloroform water. Latterly I used Schulze's phenol-glycerine mixture (phenol, crystallized, 1 grm., glycerine 200 c.c., distilled water 200 c.c.), as giving the same results and being more convenient to handle.

Nervous System.

The distribution of the nervous elements is such as one would expect from the reactions of the living animal. They are most numerous in the foot and in the head and tentacles, and are much scarcer in the middle part of the body.

The nervous cells are best seen in maceration preparations. I have found the most useful method to be maceration in Hertwig-Schneider's mixture (0·02 per cent. osmic acid, 1 part : 5 per cent. acetic acid, 4 parts) for fifteen to twenty minutes and subsequent staining in a strong filtered solution of methylene blue for three-quarters of an hour or longer. The methylene blue is dissolved until a deep blue solution is obtained. The specimen is then well macerated and several gentle taps on the coverslip are sufficient to separate the cells. By dividing the Hydra before maceration has begun a fair idea of the relative distribution of the nervous cells may be obtained.

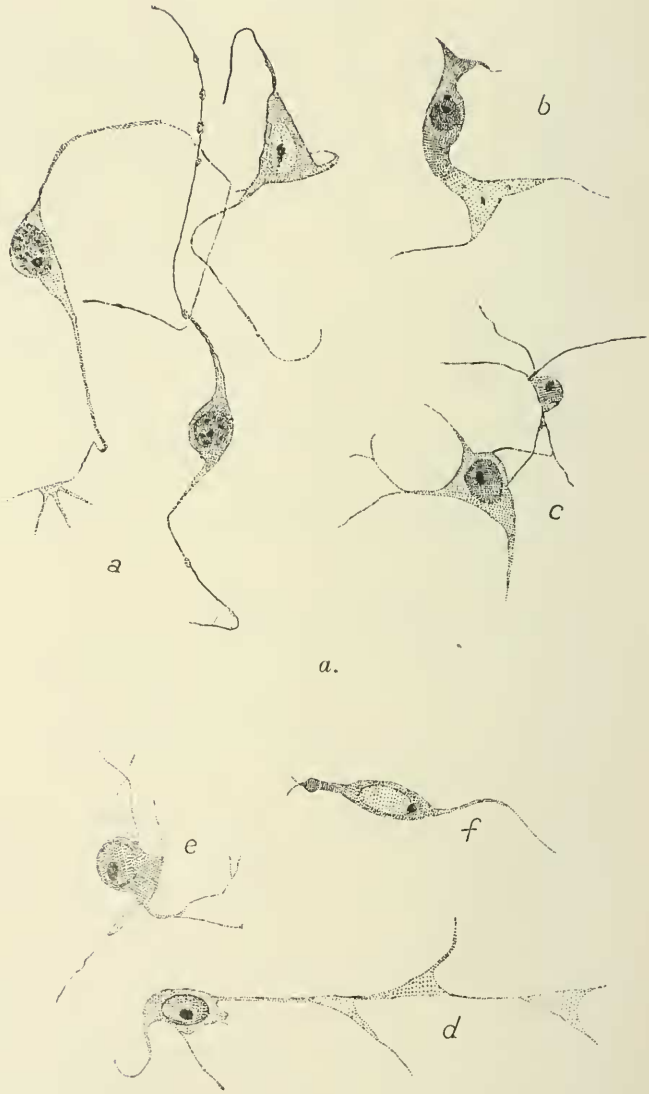
The maceration method has been largely used by Hadzi (**4**) in his work on the nervous system of Hydra. I cannot, however, confirm all his findings.

The nervous cells may be roughly divided into two types, (1) the ganglion cells and (2) cells which are more or less intermediate in form between the ganglion cell and the epithelial cell.

The former are of various shapes according to the number of processes they possess (Text-fig. 4, *a*, *c*, *d*, *e*). The nucleus stains much less deeply with methylene blue than that of the ordinary interstitial cell, as does also the nucleolus. There may be two of the latter. The cell-body usually consists of a thin layer of protoplasm surrounding the nucleus, but it is frequently prolonged at either end into a short thick process before giving off the long nerve-threads. These latter are long thin processes, often branching. Where they branch there is usually a slight swelling, and these swellings are seen along the course of unbranched processes as well (Text-fig. 4, *a* and *d*). The processes of one cell can often be seen to unite with those of another, so that the cell-body appears to lie in a network of interlacing threads. Many of the processes apparently end freely, sometimes in a small knob, while others are attached to the muscle-fibres of myoepithelial cells from which they cannot be detached by tapping on the cover-glass or by irrigation under it. The ganglion cells of the body are usually simpler and less branched than those of the head or foot.

The second type of nervous cell is long and narrow in shape, with the nucleus about the middle of the cell-body, and has a nervous process only at one end (Text-fig. 4, *b* and *f*). This may branch and sometimes it comes into connexion with another nervous cell. The other end is flattened (Text-fig. 4, *b*) or knob-like. These cells correspond to Hadzi's 'sensory cells' or 'sensory nerve-cells', but I have, as a rule, not been able to find a short projecting hair on the flattened end. In one case a knob-shaped end bore two fine hairs each ending in a little swelling, and in several other cases there were one or two short hairs (Text-fig. 4, *f*). On examining the surface

TEXT-FIG. 4.



a.

b.

Nerve cells.

of a deeply stained Hydra with an oil-immersion lens, I have not been able to find any number of projecting hairs (apart from the cnidocils) such as one would expect if sensory cells bearing hairs played a large part in the stimulation of the Hydra.

I have also tried Hadzi's vital methylene blue method (**4**) but without success. Hadzi states that his method gives good results only with H. viridis and in sunshine. In my specimens the nematocysts took up the stain strongly and the ectoderm faintly, but there was never any differential staining of the nervous elements.

It is considerably more difficult to recognize nervous cells in section, since the processes are cut short. Hadzi figures, and describes as nervous, cells which stain more deeply than the other interstitial cells and lie basi-epithelially, sending processes to the surface and in other directions. I have seen such appearances in section, but find it impossible to say whether these apparent threads are not merely strands of protoplasm belonging to the myoepithelial cells, or cut edges of cells. I have not found the sensory apparatus which he describes at the surface.

The nerve-cells probably originate from interstitial cells. Some of the latter may often be found connected to one another by short strands, and interstitial cells with short or long processes are not uncommon especially in the tissues of newly hatched Hydras. These differ little from the nervous cells except in their nuclei and in the larger amount of cell protoplasm which they possess.

The effect of various nerve poisons was tried.

Chloroform.—A weak solution of chloroform in water (which anaesthetized a Daphnia completely in a few minutes) caused a curious rhythmic contraction. The animal contracted down into a tight spiral quickly, and then slowly straightened out again. This was repeated at intervals which gradually increased from about two minutes up to fifteen or twenty minutes. Eventually it became motionless and insensitive to contact. This occurs in two hours or longer, after which

the Hydra can recover if removed to pure water. The chloroform has, however, a macerating effect, which begins to act at the tentacles.

Chloretone.—The effect of this was to make the Hydra throw out masses of endodermal cells by the mouth. It usually died.

Cholin.—Weak solutions (1 : 1,000) of this were used but were ineffective. Stronger solutions led to a half-contracted state, but the animal soon recovered in fresh water.

Curare.—A weak solution of curare was prepared by grinding up 0·1 grm. curare with 20 c.c. water and filtering. A clear yellowish solution was obtained. A Hydra was put in a small dish and this solution added till it was about half strength. For some hours the Hydra remained quite normal. After that a stimulus on any part of the body was responded to by a general contraction, and the tentacles remained half contracted. It was left in the solution over night and in the morning was found to have eaten a Daphnia which had been present; but it was very much contracted and did not respond at all to stimulation. Removed to fresh water it expanded but remained very insensitive. On examination the tentacles were found to be degenerating from their tips downwards.

The experiment was repeated with another Hydra and the same result obtained much more quickly, for in two hours the animal ceased to react to stimulation and its tentacles began to degenerate.

It is noteworthy that necrosis always begins at the tentacle tips and works down gradually, the body remaining apparently normal for some time after the tips of the tentacles have disappeared entirely.

In one case the whole head suffered necrosis and the animal remained as a closed tube for some days. It then produced two buds about the middle of the body and a third near the head region but slightly to one side. These developed and constricted off and a fourth bud appeared, again to one side of the head. As it developed it swung round so that eventually

it was in line with the main axis of the body, and acted as the true head. The curare thus appears to destroy the power of regeneration in the affected parts: possibly the interstitial cells are killed off.

Symbiotic Cells.

Since the differences between the various species of brown Hydra seem less marked than their resemblances, it is of interest to know whether, under any circumstances, a H. viridis deprived of its green cells would grow to resemble a brown Hydra.

Goetsch (**3**) obtained brown Hydras showing pathological features, which, when fed with algae, turned green. As they did so they diminished in size, budding ceased, and under natural conditions they died. Some which were fed with freshly killed Daphnia lived, and produced testes or ovaries. The symbiosis was easily lost, disappearing after four weeks in darkness. Goetsch suggests that this Hydra is a new mutant, capable of receiving the alga, which is a large form of Chlorella.

Whitney (**14**) describes a method of ridding H. viridis of its green inhabitants. He kept his specimens in a weak solution of glycerine (0·5 per cent.) for a few weeks. During this period the endodermal cells swelled up and extruded the algae, which were then thrown out by the mouth. Eventually he obtained several colourless Hydra which lived normally in the aquarium for some time without being reinfected. They retained all the features typical of H. viridis except the colour.

On January 26 I set five Hydras in a jar of 0·5 per cent. glycerine, where they were fed as usual. They budded actively. On February 13 they had increased to nine and were removed to 0·75 per cent. glycerine as the weak solution had had no effect. On March 1 there were twenty-three Hydras, still quite green, and they were removed to 1 per cent. glycerine. One was fixed and sectioned. The endoderm appeared to be quite normal in size, and the green algae were arranged as

usual all through the cell and were not collected at the distal end. On March 9 thirty-one Hydras were removed to 1·5 per cent. glycerine. In the middle of April they were still quite green.

Several Hydras were kept in the dark for the same purpose, but although the colour grew somewhat paler they all died before the green cells had been entirely lost. Hadzi (**5**) has also noted that they do not survive in darkness. Eggs, apparently colourless, which were produced in the dark, died before hatching.

Some brown Hydras were induced to swallow pieces of H. viridis by slipping the latter inside the carapace of Daphnia, but they were ejected along with the remains of the food and had no effect.

Daphnia were also fed on a pure culture of Chlorosphaera and were then given to the Hydras, but with no effect.

There have been many attempts to make a pure culture of the green organism inhabiting H. viridis. In Beyerinck's (**1**) paper on the culture of algae and lichens he states that he has been unable to obtain a pure culture of the zoochlorella from Hydra, but he adds a foot-note to the effect that he had obtained such a culture, and that the organism was indistinguishable from Chlorella vulgaris.

Later writers have made damp cell-cultures and have seen division taking place, but so far as I know there has been no large culture obtained.

I washed H. viridis in several changes of sterile water and then teased it up with needles till practically all the green cells were freed. They were then sown on Miguel solution in tubes and sporulation dishes, on Amoeba-agar, and on agar made up with Miguel solution, but in none of these was any culture obtained.

In one tube of Miguel, Chlorosphaera limicola (Beyerinck) appeared. The Daphnia on which the Hydras were fed were themselves fed on a mixed green culture which proved to contain Chlorosphaera, and the organism may

have remained alive inside the Hydra after the Daphnia had been eaten.

In damp chambers and on sterile slides the green cells remained alive for a week or more and some divided, but eventually they all died off or bacteria appeared. The cells divided either into two or three. Radais states that in a culture of Chlorella vulgaris the cells divided into four when healthy, but as the culture grew older the rate of division slowed down, and the cells divided into three or two.

When stained, the organism from H. viridis shows a large and distinct pyrenoid. The nucleus is less distinct and usually appears as an irregular ring of darkly staining material. No division stages were seen.

Taxonomy.

The number of species of Hydra has been much discussed ever since the foundation of the genus. Schulze (9) has lately divided it into three genera and about ten species. The Hydras on which I worked do not exactly correspond to any of Schulze's species but come nearest to his H. attenuata, from which they differ in being hermaphrodite. It seems to me improbable that the genus Hydra is justifiably divided up into so many definite species. Some of Schulze's species are founded on the examination of preserved specimens only. The general habit, colour, size, and so on, are used as differentiating characters, while the nematocysts are always treated as important diagnostically. The Hydras on which I worked varied considerably in size and habit, but all possessed the same kind of nematocysts. In some the egg was stuck on the side of the glass and in some it fell freely to the bottom. Considering the great variation in appearance which may take place within the lifetime of one individual, it seems unsafe to separate off as distinct species animals whose whole life history has not been completely followed through.

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